

OBSERVATIONS ON PREY CAPTURE AND ANTI-PREDATOR BEHAVIORS OF OGRE-FACED SPIDERS (*DEINOPIS*) IN SOUTHERN COSTA RICA (ARANEAE, DEINOPIDAE)

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ABSTRACT. Members of two apparently conspecific *Deinopis* populations from southern Costa Rica perform backward (aerial) strikes (in response to vocalizations and vibrating tuning forks) and forward strikes (to capture ambulatory prey). At daybreak these spiders quickly shift from foraging to cryptic behavior. This cryptic behavior, which is described and illustrated in detail, involves camouflage on a linear plant structure and/or stick mimicry. Body form, fringes of setae, palpal tarsus and claw shape, and color pattern all enhance the effectiveness of these cryptic behaviors.

The so-called ogre-faced or net-casting spiders of the genus *Deinopis* MacLeay 1839 are distinguished by remarkably large posterior median eyes and an unusual prey capture strategy. A small, highly extensible, cribellate capture web (a reduced orb-web) is constructed at nightfall, held at its four corners by the first two pairs of legs (Fig. 1), and actively manipulated to ensnare passing prey (Baum 1938; Roberts 1954; Theuer 1954; McKeown 1963; Robinson & Robinson 1971; Austin & Blest 1979; Gertsch 1979; Coddington 1986; Coddington & Sobrevila 1987; Penney & Whitehead 1995). Blest & Land (1977) have shown how the posterior median eyes, possibly the largest simple eyes of any land invertebrate, are specialized to concentrate light for nighttime visual detection of prey; and Blest (1978) has documented the spectacular and enigmatic diurnal cycle of rapid destruction (at daybreak) and synthesis (at nightfall) of the photoreceptor membrane in these eyes.

Coddington & Sobrevila (1987) showed that individuals of the Neotropical species *Deinopis spinosus* Marx 1889 can perform two quite different stereotyped attack behaviors, a backward strike to capture aerial prey and a forward strike to capture walking prey. In so doing, these authors resolved a controversy between Theuer (1954), who had described only backward strikes in *D. spinosus*, and Robinson & Robinson (1971), who observed forward strikes and were unable to elicit backward (aerial) strikes in their study

of another species, *Deinopis longipes* F. O. P.-Cambridge, in Panama. Coddington & Sobrevila demonstrated that the backward strike is triggered by airborne vibrations, presented evidence consistent with Robinson & Robinson's conclusion that the forward strike is triggered by visual stimuli, and predicted that other *Deinopis* species would be found to exhibit both types of capture behavior.

Literature references to the cryptic behavior of *Deinopis* spiders during the daytime are brief, in part because these behaviors are so effective (Baum 1938; Theuer 1954; McKeown 1963; Robinson & Robinson 1971; Austin & Blest 1979; Gertsch 1979). Three such anti-predator postures have been observed (pressed flat against a branch, suspended head downward in midair with legs extended away from the longitudinal axis of the body in four tight pairs forming a cross, or hanging head downward in midair with legs I and II protracted and apposed in front and legs III and IV protracted and apposed behind the body to form a single linear "stick"), but no one has described the form of these anti-predator behaviors or associated structural design features in detail. Ackerman's (1926) description of twig/bud mimicry in *Menneus camelus* Pocock 1902 is, to our knowledge, the most detailed observation to date of a deinopid anti-predator tactic.

Our brief field study of the behavior of two Costa Rican *Deinopis* populations was designed to achieve two main objectives: 1) de-

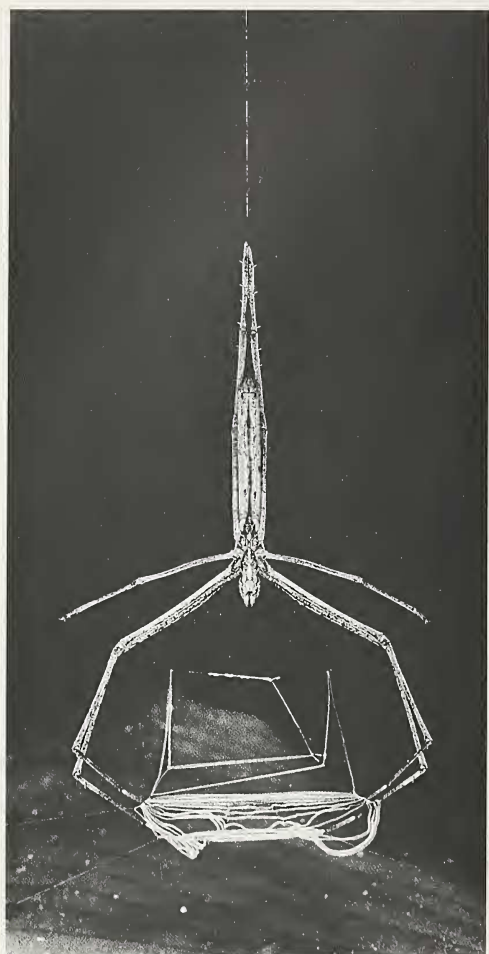


Figure 1.—*Deinopis* spider at Las Cruces in foraging posture above leaf surface.

termine whether these spiders perform backward strikes, and, if so, what stimuli trigger such strikes; and 2) describe in detail the diurnal anti-predator behavior of these spiders.

METHODS

We observed *Deinopis* from 5–12 March 1995 along trails in second growth forest at two locations in Puntarenas Province, Costa Rica: 1) the Las Cruces Field Station of the Organization for Tropical Studies near San Vito, and 2) above Rio Sierpe Lodge near the mouth of the Rio Sierpe on the Osa Peninsula. The nine spiders observed in this study, four from Las Cruces (spiders A, B, C, and D) and five from Rio Sierpe (spiders E, F, G, H, and I), were discovered at night in their prey capture posture (Fig. 1). Two (A and I) were pen-

ultimate males and the rest were probably penultimate females. Two were collected from each site and were examined by Brent Opell, who concluded that both populations probably represent the same undescribed species. These four specimens have been deposited in the Museum of Comparative Zoology.

When observing nocturnal behaviors, we used headlights with lenses covered by one (first night) or two (subsequent nights) layers of red cellophane. In order to determine whether this species performs the backward (aerial) attack, we tested six of the spiders with a tuning fork stimulus (256 Hz) after the method of Coddington & Sobrevila (1987). The tuning fork was positioned about 10 cm behind the capture-ready spider. A series of ten stimuli, five vibrating (experimental) and five not vibrating (control), were presented in alternating sequence to each spider with about 10 sec between successive stimuli. To observe the form and timing of the transition from nocturnal foraging behavior to diurnal cryptic behavior, we commenced observing a spider at about 0400 h, almost one hour before dawn. Still photographs were used to document cryptic postures.

PREY CAPTURE BEHAVIOR

The postures of capture-ready spiders and the form of the webs (Fig. 1) were virtually identical to those described by Robinson & Robinson (1971) for *D. longipes*. All capture-ready spiders were suspended above living or dead (lying on the ground) horizontal leaves. The capture web was held either parallel or perpendicular to the leaf surface, usually about 15–30 mm above it.

The first author's exclamation upon discovering the first spider triggered a backward (aerial) strike, and the short series of excited vocalizations that followed triggered three more such strikes in quick succession. Subsequent observations of other individuals confirmed that this species, like *D. spinosus* (Coddington & Sobrevila 1987) and two species of Australian deinopids (Austin & Blest 1979), responds consistently with backward strikes to hums and other vocalizations generated from a distance of up to 50 cm or more.

In the tuning fork stimulus trials (Table 1), 30 of the 40 presentations of a vibrating fork triggered strikes (all of which were backward strikes) and none of the 40 presentations of a

Table 1.—Results of tuning fork stimulus presentations to Costa Rican *Deinopis* spiders. See text for description of procedure.

Series #	Spider	No. of stimulus presentations		No. of strikes	
		Vibrating	Non-vibrating	Vibrating	Non-vibrating
1	A	5	5	5	0
2	A	5	5	5	0
3	C	5	5	4	0
4	D	5	5	5	0
5	E	10	10	6	0
6	H	5	5	3	0
7	I	5	5	2	0

non-vibrating fork triggered a strike. These results, in conjunction with the responses to vocalizations described above, show that airborne sounds and/or accompanying air currents are sufficient to stimulate the backward strike, and support the hypothesis that this mode of attack serves to capture flying insects. Like Coddington & Sobrevila (1987), we observed habituation (and/or fatigue) of this response; the first strike of a series was the most energetic strike (spiders A, D, and E each performed two strikes in response to the initial vibrating stimulus) and later strikes were less energetic than earlier ones in a given series (spiders E, H, and I failed to respond to the last 4, 2, and 3 presentations). Candidate sensory mechanisms which may permit *Deinopis* to detect these airborne vibrations include trichobothria and slit sensilla, both of which have been shown to play this role in other spiders (Barth 1982). Receptor ablation experiments could be used to test these hypotheses.

The aerial strike is very quick, and it is therefore difficult to observe and describe its mechanics without high speed movie or video cameras. In general, though, these strikes closely resembled the description and photos presented by Coddington & Sobrevila (1987). The spider's prosoma rotated backward, up, and away from the substrate as its snare was expanded by extension of legs I and II.

We observed two forward strikes like those described by Robinson & Robinson (1971) and Coddington & Sobrevila (1987), each in response to insect prey (a roach and a grass-

hopper) we encouraged to walk on the substrate below two different spiders. Both prey were wrapped but only the roach was eaten; the grasshopper was eventually released (rejected). Two spiders were observed feeding (in their foraging position) on prey items. Spider A was feeding on a 6–7 mm long beetle and spider E was feeding on a worker leaf cutter ant (*Atta*). The latter, and probably the former, would have been captured by forward strikes. We observed spider A use its pedipalps to bat at a small fly (about 2 mm long) that hovered and landed on the beetle; jerking movements of legs I and II also appeared to be responses to this probable kleptoparasite.

DIURNAL ANTI-PREDATOR BEHAVIOR

We observed spiders shifting from nocturnal to diurnal behavior 12 times over the course of our study. Spiders A–D were each observed doing this twice and spiders E, F, G, and I once each. We recorded the duration of this shift (from the onset of web takedown to completion of the cryptic posture) only five times (B = 3–4 min, E = less than 1 min, F = 28 sec, G = about 30 sec, I = 1.5–2 min), but recollect that none of the other seven observed shifts took more than 5 min except for the time that spider A was feeding on a beetle at the onset of dawn. Web takedown, which consisted of consolidating the capture web and at least some of the support elements, applying this package of silk to the mouthparts, and apparently digesting it, took from 20 sec–3 min. The spider then quickly climbed to its daytime resting spot by following a silk guideline and, with no more than a brief period of localized orientation and settling activity, assumed a cryptic posture. There was little variation in the time of day when this shift took place; the time when a spider assumed the cryptic posture ranged from 0455–0527 h (mean and SD = 0509 h \pm 18) for the 11 instances when a spider was not feeding on prey. The single exception involved spider A, which moved to its daytime site at 0504 h but continued feeding in a partially cryptic posture well past daybreak and became fully cryptic at 0542 h, much later than its shift to a cryptic posture the following day (0455 h).

Perhaps the environmental cue which triggers this shift is the increase of light intensity to a particular threshold level or rate of increase at dawn; we were able to first detect

increasing light at about 0455 h each morning. It is also possible that the foraging-to-crypsis shift is a circadian rhythm entrained by day-length. The only other potential cue perceived by us was the predictable and rather sudden onset of bird and howler monkey vocalizations at about 0515 h, but these events were too late to account for most of the observed shifts and no mechanism has been demonstrated in spiders for detecting such distant sounds.

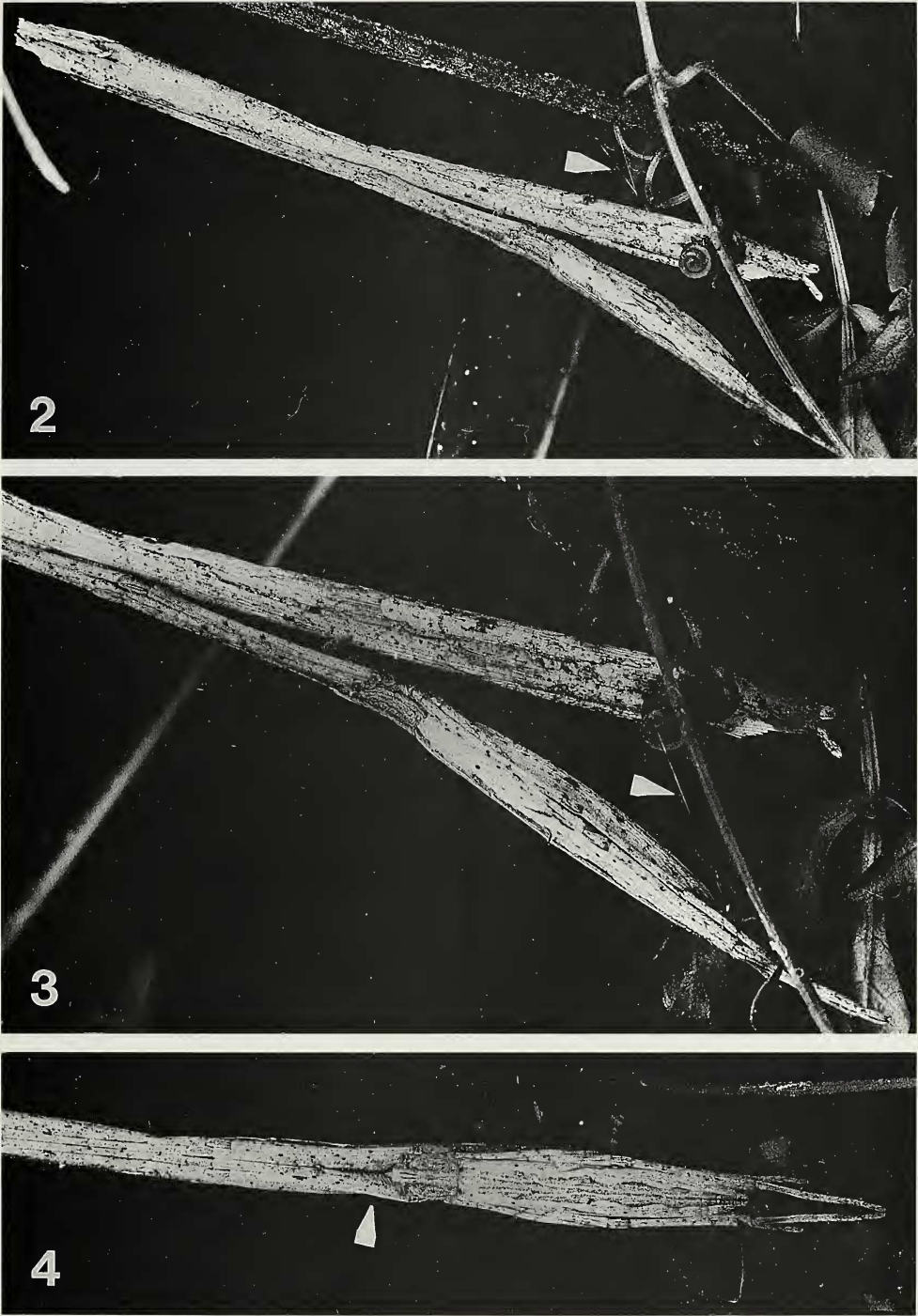
Typically, as in *D. spinosus* (see Theuer 1954), the hiding site is close to the foraging site; the distance between these sites was recorded for five spiders and ranged from 25–80 cm (mean and SD = 58 ± 21). Some site tenacity was observed during our short study. Spiders A, B, and C each foraged and hid in the same locations for the three nights and two days they were observed. Spider D likewise used the same foraging and hiding sites during the two days it was observed. Spiders E and G both moved to new but nearby sites during the second day of observation. Only spiders F and I moved so far that they were not found after the first day of observation. The presence of silk strands anchoring otherwise unattached pieces of vegetation which served as hiding substrates suggests that these spiders sometimes improve their hiding sites (Fig. 2).

Behavior, anatomy, and pigmentation all contribute to the remarkable diurnal crypsis of this spider. Assumption of the cryptic posture at dawn always involved attachment to a substrate, usually a linear plant structure (twig, vine stem, or petiole), typically a dead (brown) (Figs. 2–9), less often, a living (even green) one (Fig. 10). Most commonly the spider aligned its whole body and legs parallel to and against the substrate and appeared to become part of that substrate (Figs. 5–9), a strategy of camouflage or concealment (Robinson 1973, 1985). Less often, much or nearly all of the spider was positioned well away from the attachment substrate (Figs. 2–4, 10), and the spider mimicked a dead twig, relying on disguise rather than concealment (Robinson 1973, 1985). Attachment to the substrate was typically via silk (spinnerets to substrate) (Figs. 2–4) and usually by leg and/or palpal claws as well (Figs. 2–10). Most spiders were oriented head down (Figs. 5–11), but one was inclined in a slight head-up position (Figs. 2–4). Always legs I and II were protracted anteriorly and apposed and legs III and IV were

protracted posteriorly and apposed along the sides of and beyond the tip of the abdomen so that the spider became a long slender stick-like unit (Figs. 2–11). Sometimes the spider “settled” into this posture with regular wave-like undulations of its legs and body; at other times the shift to this posture was more sudden and direct. While a given spider often hid at the same location for at least two consecutive days, it did not necessarily adopt the same posture on the same substrate (compare Figs. 2 and 3 to Fig. 10). This plasticity in the cryptic behavior of individual spiders is consistent with Robinson’s (1985) suggestion that concealment is a “preadaptation to plant part mimicry.” An individual which is positioned as in Figs. 2 and 3, so that part of its body is camouflaged on a stick and part is mimicking a stick, may illustrate an adaptive intermediate evolutionary step between pure concealment and pure stick mimicry.

Several anatomical design features contribute to camouflage and stick mimicry in this species: 1) The long slender body and legs produce a sticklike form, 2) the flat and posteriorly truncate carapace and anteriorly low and truncate abdomen lower the body profile and help conceal the transition from carapace to abdomen, and 3) the fringes of long setae proximally on the prolateral surface of the first femora and at the anterior median edge of the carapace fill and thus hide much of the gap between the femora (Figs. 4–6). 4) The tip of each palpal tarsus curves prolaterally and the palpal claws are long, features that help these claws grip and hold the body against cylindrical substrates (Figs. 2, 3, 7, 8). The spider’s variegated light to dark brown pigment pattern closely resembles the coloration of many dead branches, vine stems, and petioles (Figs. 2, 3, 5–9).

When its body or its substrate is touched, a cryptic spider typically increases its crypsis by pressing its legs more tightly together and against the body, and, if positioned against a substrate, by flattening itself more tightly against that substrate (Figs. 5–8). Such a posture adjustment can effect a dramatic improvement in crypsis; sometimes it makes the spider temporarily disappear from view! When we tried to grasp one cryptic spider, it dropped several cm from the substrate and became sticklike while hanging free and motionless in midair from its dragline (Fig. 11).



Figures 2-4.—*Deinopis* spider C at Las Cruces; three views of spider in cryptic posture. Spider is attached by the claws of legs I and II, palpal claws, and dragline (see arrow in Figure 3) to undersurface of dead piece of stem or petiole which is suspended from a vine by silk (see arrow in Figure 2); 2, 3, Side view; 4, View from below (arrow points to gap between front femora, which is partly filled in by fringes of long setae on femora and caput).



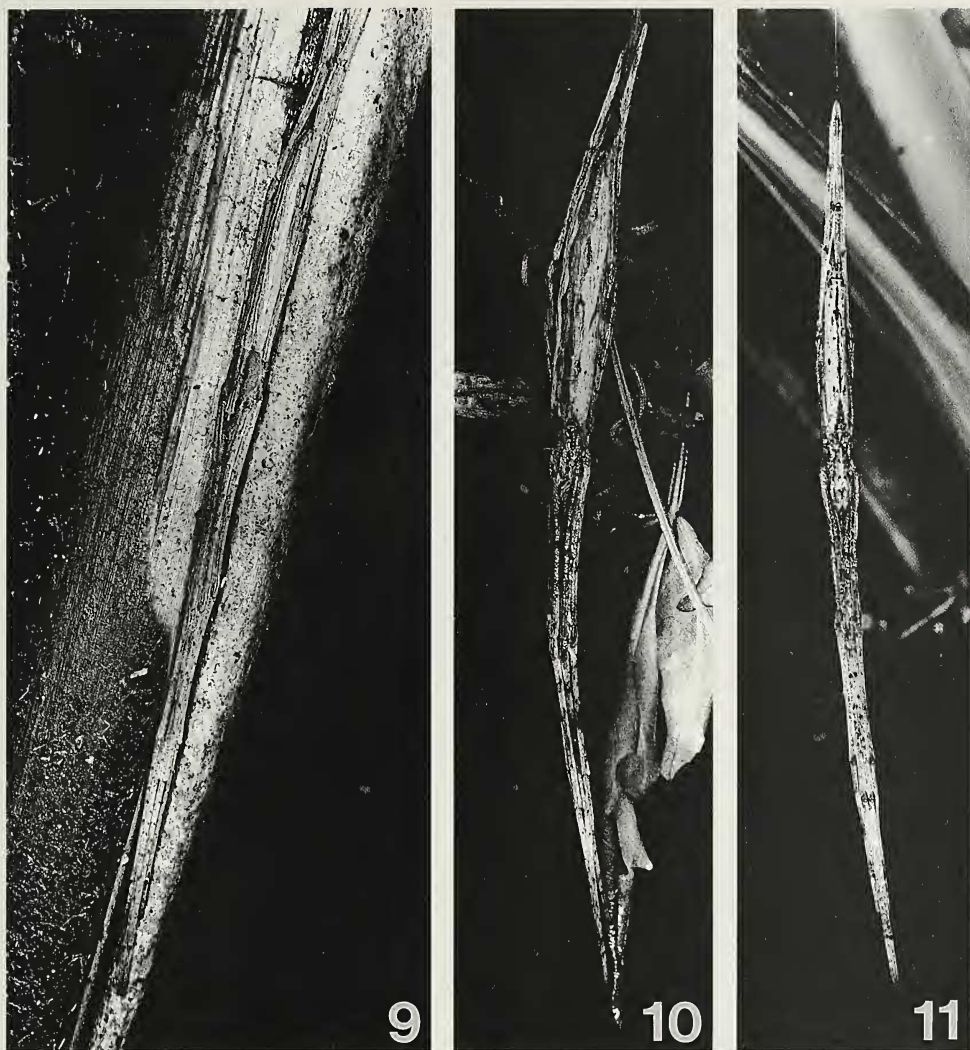
Figures 5–8.—*Deinopis* spider E at Rio Sierpe; four views of spider facing downwards in cryptic posture on dead stem. 5, 6, Dorsal views; 5, Posture before stem is touched by observer; 6, Posture after stem is touched; 7, 8, Side views; 7, Posture before stem is touched by observer; 8, Posture after stem is touched. Arrows point to junction between prosoma and opisthosoma.

The defensive effectiveness of these behavioral and structural design features against visual predators is suggested by how much more difficult it is to find these spiders in daylight than at night. Despite careful searching, we were unable to find these spiders by day; this matches the experience of other authors with other deinopid spiders (Akerman 1926; Baum 1938; Robinson & Robinson 1971; Coddington & Sobrevila 1987; Penney & Whitehead 1995). On six occasions (three different spiders) we asked a person to locate one of our subject spiders during the daytime after defin-

ing a roughly $20 \times 20 \times 20$ cm cubical search space containing the spider. None of the four people presented with this challenge succeeded. We suspect that the key selective agents responsible for the evolution and maintenance of this suite of cryptic defensive traits are to be found among diurnal insectivorous wasps, lizards, birds, and monkeys.

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Figures 9–11.—*Deinopis* spiders at Las Cruces in cryptic postures; all facing downwards. 9, Spider R in longitudinal depression on stem; 10, Spider C hanging from slender vine and holding to leaf edge with anterior leg tarsi; 11, Spider D hanging motionless from dragline after being forced to drop from cryptic posture on plant.

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